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Editorial: Cognition, foraging, and energetics in extant and extinct primates

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Editorial on the Research Topic
Cognition, foraging, and energetics in extant and extinct primates

Within the framework of optimal foraging theory (Stephens and Krebs, 1986; Pyke, 2019), primates living in complex and fluctuating environments are likely to mobilize cognitive skills—such as episodic or long-term memory, planning and value-based decision-making—that allow them to exhibit more efficient foraging decisions and strategies (Janson, 2019; Trapanese et al., 2019; Garcia et al., 2021). These strategies toward optimizing energetic balance (i.e., maximizing benefits while minimizing costs and risks associated with the exploitation of resources in the environment) are suggested to vary at the interspecific level but also to be constrained—or indeed enhanced—by the social context.

Nevertheless, there is still much we do not know about the cognition supporting foraging behavior in primates, and a collective and concerted effort toward filling the gaps was needed. This Research Topic has brought together researchers from diverse disciplines including animal cognition, behavioral ecology, paleoanthropology, archeology, and ethnoecology. It aimed to illustrate our current understanding of the diversity in primate foraging strategies and associated cognitive abilities in different socio-ecological contexts, both past and present. The issue is composed of contributions on modern primates (including humans) as well as extinct hominins, from laboratory settings and from fieldwork, and taking empirical, theoretical, or conceptual approaches to provide a more complete understanding of foraging cognition across the primate order. Overall, these studies highlight the extraordinary variation existing in several key cognitive processes mobilized for foraging, and point to socio-ecological factors that drive the evolution of foraging decisions at the individual and collective levels. Foraging behaviors draw on cognitive skills to make complex decisions (e.g., in modulating navigation strategies or travel paths for exploiting sparse or ephemeral resources: Janmaat et al., 2014; Green et al., 2020) contingent on ecological challenges but also on long-lasting social interactions with competing or cooperating conspecifics (see Garcia et al., 2021 for a review). Four articles in our collection illustrate the complexity of foraging decisions related to the optimization of cost-benefit ratios.

Two focus on "high-yield, high-risk" resources, e.g., aquatic resources and meat fat, both hypothesized to have played significant roles in human evolution (Snodgrass et al., 2009; Cunnane and Stewart, 2010). In their review, de Chevalier et al. suggest that aquatic foraging could have emerged in several non-human primate species at sites where the local

cost-benefit trade-offs favor aquatic vs. terrestrial food items. Moreover, they suggest that the unique intensification of aquatic resource consumption in hominins has led to true coastal adaptations, expansion of their niches and diversification of their diets. In another paper, Daujeard and Prat review the costs and benefits of meat and fat consumption during the course of human evolution, in terms of energetic impact and social aspects (social cooperation, food sharing). They also point out the difficulties and limits encountered in this research area, notably by the scarcity of archeological evidence but also by the silent influences of culture and symbolism on food choices. A third article (Gallois and Henry) explores the costs of activities related to gathering and plant foods acquisition in the livelihood of a mixed economy society, the Baka forager-horticulturalists in Cameroon. They show that gathering activities are energetically costly, with higher energy expenditures than for hunting and fishing activities, and that the costs associated with gathering depend on the targeted plant foods. Finally, by using an experimental approach in wild vervet monkeys, Arseneau-Robar et al. show that these monkeys make foraging decisions based on a balancing of costs and benefits, i.e., minimizing travel time and distance, but also ensuring they get access to their preferred food rewards when competitors are present. By taking into account complex social contexts in the planning of their foraging trips, they are capable of quickly assessing the risk of competition and modifying their route accordingly, showcasing the impressive complexity of foraging decisions in this species.

Three further papers provide detailed examinations of food-related decision-making in both human and non-human primates. Such decisions can be crucial components of fitness: detecting, discriminating, and efficiently exploiting known resources are fundamental skills for survival. At the same time, identifying novel food items can not only buffer individuals in times of low resource availability, but also potentially provide individuals with a selective advantage over others in the population, particularly when environments change and novel foods appear while familiar sources disappear (Webster and Lefebvre, 2001; Amici et al., 2020).

In this vein, Ventricelli et al. experimentally examine captive capuchins' responses to novel foods, predicting that neophobia toward these items will vary according to three distinct effects: experience, risk-aversion, and social rank. While none of these effects materializes in the data, the study does highlight effects of social rank and sex on neophobia. These likely relate to the nature of competitive interactions around both familiar and novel foods in the experiment, and have implications for the dynamics of incorporating novel foods into the dietary repertoire of wild populations. Shifting to the wild, Matsuda et al. examine food selectivity in guerezas in Uganda and show that neither the chemical and mechanical properties of leaves, nor their digestibility and abundance influence the guerezas' choices. However, they do identify differences in foraging effort devoted to leaves based on their protein content and toughness. Examining related questions in humans, Veen et al. report on the foraging behavior of Mbendjele BaYaka forager children in the Republic of the Congo. In contrast to the diet of other primates, the human diet is characterized by a diverse variety of high-quality and difficult-to-acquire foods (Milton, 1999; Kaplan et al., 2000). The authors find that BaYaka chilDren are able, already from an early age, to correctly identify foraging related plant species, and their botanical knowledge increases with age. Furthermore, they exhibit early sex-related specialization in foraging skills. Crucially, the study also documents how the diet of the BaYaka is changing along with their increasingly horticultural lifestyle, further highlighting that the effects that such shifts may have on the development of children's spatial and foraging cognition are as yet unknown.

Finally, two papers in our collection review some of the unique foraging challenges associated with the primate lifestyle. Harel et al. outline how moving through canopy environments makes specific demands on individuals' sensory, cognitive, and locomotory skills. The "networks of branching pathways" they need to negotiate in order to travel between destinations require individuals to weigh up the risks, costs, and rewards of multiple available options. The authors further highlight that the structure of canopy environments may also influence primate groups' capacity for coordinated action and cohesion, phenomena that become central in Williams et al.'s extensive review. This contribution provides an overview of the impact that sociality and the need for collective action may have on how primates tackle foraging challenges. Moving and foraging in groups is associated with increased competition, exacerbated by dominance asymmetries, leading to inequalities, intra-group conflict, and the differential balancing of benefits and costs across group members. Yet, through both democratic and despotic inputs, collective behavior can be highly efficient under many circumstances. The authors draw analogies with research in human organizational psychology to encourage a better understanding of the effect of group size and group composition on collective decision-making, collective movement, leadership, knowledge pooling, and coordinated action.

Together, our nine contributions showcase the diversity in primate foraging strategies and associated cognitive abilities, painting a nuanced picture for what foraging cognition is. Such work has opened new exciting questions that merit investigation and we hope that the contributions contained within this special issue will stimulate discussion and promote more research. Given ongoing habitat destruction and globalization (Estrada et al., 2017), one can wonder what the consequences will be of the decrease in species diversity and required botanical knowledge on the cognitive development of modern human foragers as well as other primates.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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